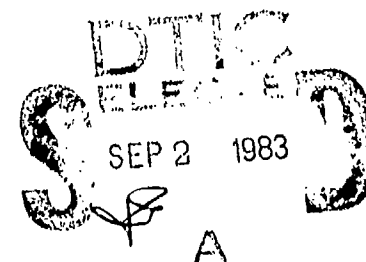NAMRL Monograph 30

FIGURAL AFTEREFFECTS: AN EXPLANATION IN TERMS OF MULTIPLE MECHANISMS IN THE HUMAN VISUAL SYSTEM

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ABSTRACT

As an alternative to the classical explanation of figural aftereffects (FAE), it was hypothesized that FAE are due to changes in the relative activities of multiple mechanisms tuned to specific features of the stimulus pattern. Changes along the stimulus dimensions of size and orientation were studied. The rationale was that prolonged exposure to an inspection figure (IF) of a particular size or orientation would change the appearance of a test figure (TF) to the extent that these two figures stimulate the same mechanism. Following selective adaptation to a particular IF, subjects were required to make size or orientation judgments with the size or orientation of the IF serving as the anchor for these judgments. Results indicate that there was a particular range of TF size or orientation over which a given IF would produce perceptual changes. TFs outside this range were not affected. Findings were compared with the classical explanation and the role of multiple mechanisms as a basis of FAE was elaborated.

INTRODUCTION

MECHANISMS IN THE HUMAN VISUAL SYSTEM

Various theories have been proposed to account for how information concerning the stimulus form is processed. Classical approaches, i.e., Gestalt (15), and lateral inhibition (10), (11), (12), have traditionally emphasized the processing of the entire form when explaining various visual phenomena. The emphasis from current psychophysical (8) and electrophysiological data (13, 14), however, is on the analysis of component parts of the stimulus form. The purpose of the present experiments will be to examine the efficacy with which these different approaches can account for the phenomenon of figural aftereffects (FAE).

A large number of studies have noted that following prolonged visual exposure to an inspection figure (IF) there are pronounced phenomenological changes in the appearance of a subsequent test figure (TF). Kohler and Wallach (16) first described these changes in the appearance of TFs, termed figural aftereffects, and noted that they occur along a number of dimensions, such as size of the test figure and test figure shape.

Kohler and Wallach (16) explain FAE by positing the existence of a homogeneous chemical medium consisting of a polarizing current. Following prolonged stimulation to an IF, this chemical medium becomes satiated and resistant to further stimulation from objects. When a TF is presented subsequently, Kohler and Wallach (16) maintain that the figure will affect portions of the medium not previously stimulated. Thus, the figure will appear to be both in a different spatial location and distorted in shape.

A critical feature of this explanation is the displacement effect. Kohler and Wallach (16) maintain that inspection of a figure will cause a TF, placed an optimal distance from the inspection location, to be displaced away from the boundary of the IF. The magnitude of these displacements is therefore a function of the distance between the two contours. Effects are maximal when the two contours are a "short distance" apart; if the distance between the two contours is increased or decreased, the amount of this displacement decreases markedly. This lack of linearity between distance and the amount of aftereffect was termed the distance paradox in that there is an optimal distance between the contours of the IF and TF after which the extent of the aftereffect is decreased. Displacements and their corresponding size changes are distributed with distance between the contours of the IF and TF.

A serious problem with the Kohler and Wallach (16) physiological explanation of FAE is that there is no physiological evidence for the polarizing currents essential to the theory. An alternative explanation for the FAE phenomenon (9), which makes the same predictions as the Kohler and Wallach (16) hypothesis, invokes the classical processes of lateral inhibition and light adaptation to account for the occurrence of FAE. Theoretically, the IF acts by producing regions of differential light and dark adaptation. Thus, when the TF is presented, the afterimage of the IF (which is identical, from a neural point of view, to the distal stimulus) exerts inhibitions by subtracting excitation from the TF's distribution of excitation. Since lateral inhibitory mechanisms are sensitive to the distance between objects, the section of the distribution closer to the peak of this excitatory ridge (i.e., closer to the contour of the IF) is inhibited more than those sections further away. Ganz (9)

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acccunts for the distance paradox by assuming that at small distances contours summate their excitation.

A similar aftereffect to those described by Kohler and Wallach (16) and Ganz (9) was reported by Blakemore and Sutton (3). Following prolonged inspection of a suprathreshold grating pattern of a particular spatial frequency, test gratings of a lower frequency presented to the same retinal area appeared to be even lower in frequency, while those of a higher frequency appeared even higher. Blakemore and Sutton (3) explained their findings on the basis of a change in a distribution of activity in the population of frequency detecting mechanisms (2, 18), in proportion to the neuron's sensitivity to the particular gratings' frequency. Subsequent studies have provided further evidence for the presence of frequency detecting mechanisms critical to this hypothesis (6, 7, 19). Prolonged adaptation acts to reduce the overall sensitivity of these neurons. The specific frequency to which the neurons are most sensitive is not affected, however. Therefore, when a test grating of a somewhat different spatial frequency is presented, the distribution of neuronal activity is shifted away from the adapting frequency, causing a perceptual change in the appearance of the test grating.

In their discussion, Blakemore and Sutton (3) suggested that the classical FAE could be explained on the basis of a change in the activity of a population of mechanisms sensitive to specific IF parameters such as size. The present experiments, which are analogues of the Blakemore and Sutton (3) study, used the classical non-repetitive FAE stimuli to test Blakemore and Sutton's suggestion that selective shifts in the distribution of activity in mechanisms sensitive to specific stimulus parameters may account for the FAE phenomenon.

<center>EXPERIMENT 1</center>

Experiment 1 was designed to test Blakemore and Sutton's (3) idea that FAE are size specific and proceeded within the classical FAE paradigm with one major exception. The classical experiments have always obtained the maximum amount of displacement at some critical distance. In those experiments only the to-be-judged dimension was varied. In the present experiment, however, the vertical contour distance between a particular TF and the IFs remained constant (see Figure 1). The horizontal dimension was varied. Therefore, the prediction from the classical theories is that there will be no change in the magnitude of the aftereffect regardless of a change in the distribution of inspection flux. However, multiple mechanism theory predicts that each IF will shift the distribution of activity of size detecting mechanisms differently. Therefore, different perceptual changes for each IF condition is predicted for each of the TFs.

METHOD

Apparatus.

The basic piece of equipment used in both experiments was a modified free viewing optical system diagrammed in Figure 2. A single tungsten filament lamp served as the light source for the entire system. Neutral density filters placed in both pathways insured that each stimulus was viewed at minimal contrast levels. Stimuli were held at 1.5 log units above each S's threshold to insure that after-images would not confound the results of the experiment. The passage of light

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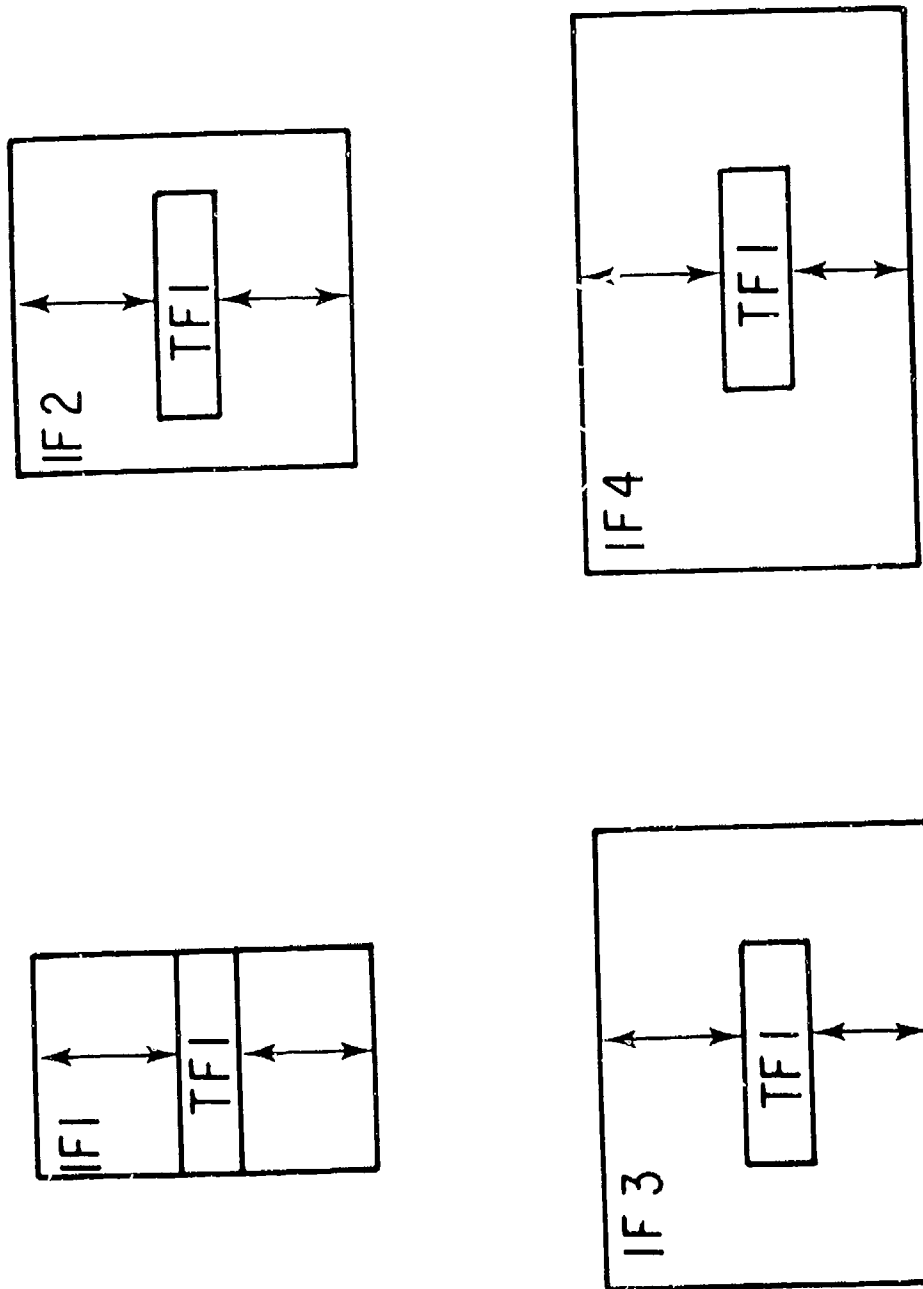
Figure 1. An example of how the contour distance remains constant across inspection figure (IF) conditions for each test figure (TF) in Experiment 1.

MIRROR I   LENS   NEUTRAL DENSITY FILTER 2
            3
                              LIGHT SOURCE
         SHUTTER 2   SHUTTER I

                              NEUTRAL DENSITY
                              FILTER I

                              LENS I

                              TEST STIMULI

                              BEAMSPLITTER
                    LENS
MIRROR 2   4
ADAPTING STIMULUS   LENS 2

              VIEWING SCREEN

Figure 2. Schematic diagram of the optical system used in
          Experiments 1 and 2. Not to scale.

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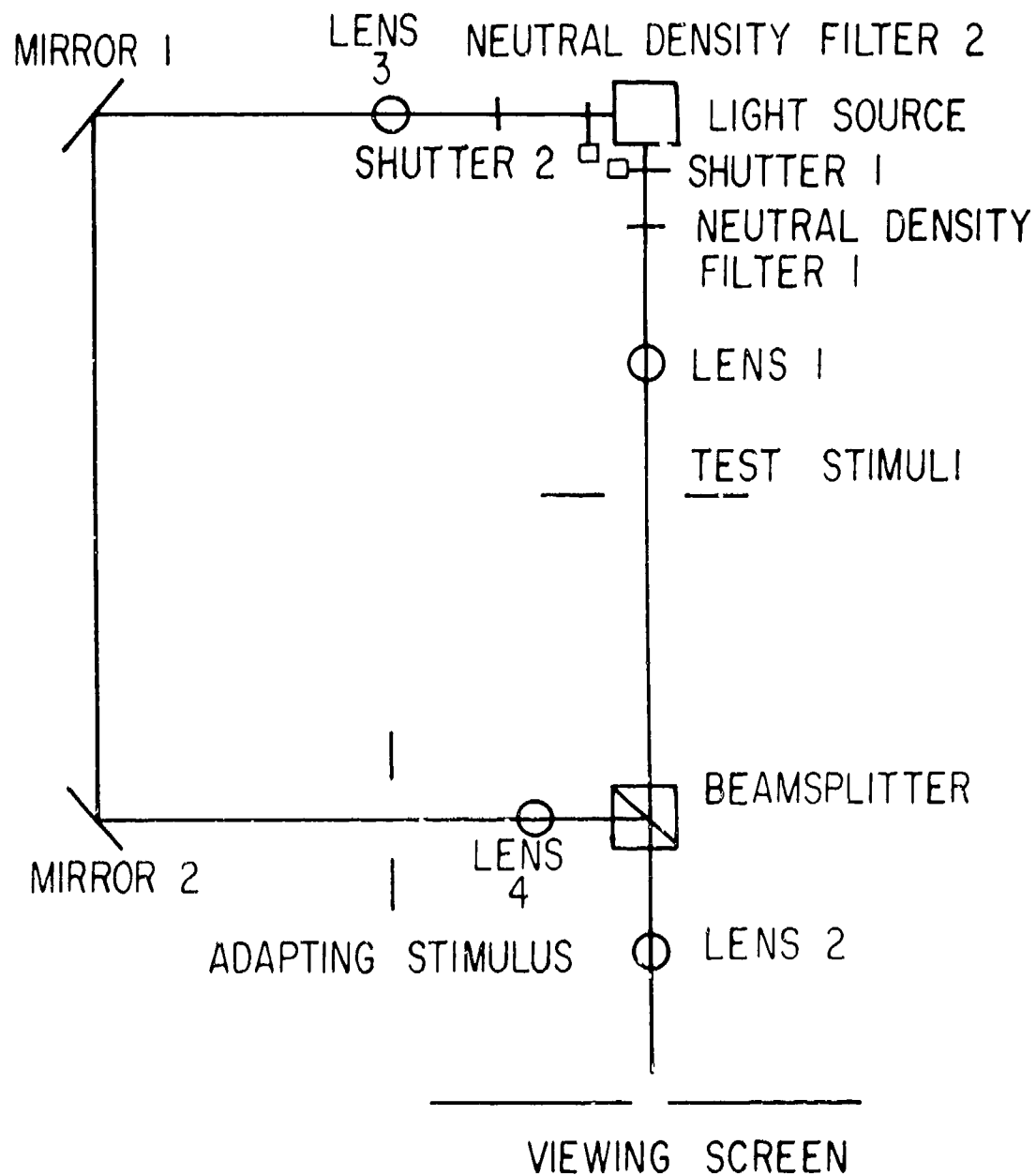was controlled by Shutters 1 and 2 and the light was imaged along the optical axis in each channel by Lens 1 and Lens 3 which were placed at their focal lengths of 193 mm from the source. The apertures which formed the test stimuli were placed around the circumference of a wheel mounted on the shaft of a rotary stepping motor located 16.50 cm in front of Lens 1 which allowed for control of trial-to-trial stimulus changes. In the adapting pathway, Channel 2, Mirror 1 reflected the light 90° onto Mirror 2 which again reflected the light 90° to form the adapting pathway. The adapting stimulus was placed 20.95 cm in front of Mirror 2. Both paths were combined on an opal glass viewing screen by a beamsplitter placed in front of Lens 2 in the test pathway 73.66 cm in front of the $\underline{S}$'s eyes. Therefore, both the test and adapting stimuli appeared in the same spatial location on the screen. A low contrast fixation point on the screen signaled the location of the stimuli while a headrest immediately in front of the $\underline{Ss}$ enabled them to maintain a stable fixation throughout the entire experiment.

Subjects. The $\underline{Ss}$ in both experiments were well practiced in visual observation and familiar with the type of response required. However, they were all naive with respect to the purpose of these experiments. In Experiment 1 three subjects (JW, KW, PZ) were used.

Stimuli. The IFs and TFs were homogeneous patches of light subtending a maximum of 4° of visual angle. A range of 450 to 7200 min^2 of visual angle was subtended on the retina. The height of the four IFs was held constant at 60 min (the height of the tallest TF) while the IF width varied from 30 (IF1) to 120 (IF4) min in 30 min of arc increments. The width of the four TFs was held constant at 30 min (the width of the smallest IF) while the height varied from 15 (TF1) to 60 (TF4) min in 15 min of arc increments.

Procedure.

Using a selective adaptation procedure (described in detail by Bagrash (1), $\underline{Ss}$ were presented with an IF of a particular width and then with a series of four TFs. The psychophysical method was a magnitude estimation procedure with the IF height serving as the anchor for the scale. Subjects were instructed that the IF height was equal to "100" and were required to rate the height of the TF as a percentage of the height of the IF. Each $\underline{S}$ was first presented with a series of control conditions which differed from the subsequent experimental sessions in that there was no prior adaptation to a particular IF before the height estimations were made. In the control conditions $\underline{Ss}$ were presented with the IF standard only four times during the session to insure that no aftereffects would confound the results of the control condition.

In each experimental session one of four different IF areas was presented and 200 trials were given in two blocks of 100. The IF remained the same within each session since different IFs may cause different changes in the pattern of activity of size detecting mechanisms. After the $\underline{S}$ became dark adapted there was a five min. period of adaptation to the IF after which the run proper was commenced. Over the course of the experiment each of the four IFs was seen by each $\underline{S}$ in four experimmental sessions. Order of presentation of the IFs was presented equally often and randomly intermixed in order to alleviate the possibility of order effects. Responses were made during a 2 sec interval following TF presentation. Prior to the pre-

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sentation of the second block of trials in each session, S readapted to the IF for 2 min. to insure that the selective adaptation effect remained constant.

Results

Data were transformed by determining the geometric mean height judgments for the TF in the IF conditions for both the unadapted and adapted judgments. The first part of the experiment consisted of the S making a series of unadapted judgments of the height of the TF relative to that of the IF. JW and KW consistently rated the unadapted heights as being their objective heights. No variance was noted in these data. Considerable variance was noted in the data for PX whose ratings were also much different than the TF's objective values.

Results were plotted as a series of difference scores. Positive numbers indicate that a particular TF was judged larger following adaptation while negative numbers indicate that the figure looked smaller than its control following adaptation. These difference scores are plotted in Figures 3, 4, and 5 in order to demonstrate that different patterns of displacement were obtained in various IF conditions. An interesting point to note from these figures is that the largest and smallest TFs were consistently rated by JW and KW as being much larger following adaptation while the two intermediate size TFs consistently decreased in rated size. These same changes were not noted for PZ.

A significant main effect of IF, $F_{(3,27)} = 32.670$, $p < .001$, was noted for JW. No effect due to TF was noted, nor were any interactions between IF and TF found. For KW an interaction between the IF and TF was noted, $F_{(3,27)} = 2.974$, $p < .05$. Analyses of the simple main effects revealed that for the intermediate size TFs the judged length of the figure declined as the IF width increased, (TF2, $F_{(3,27)} = 3.520$, $p < .05$; TF3, $F_{(3,27)} = 12.518$, $p < .001$). There were no significant effects of IF width on the judgment of TF height for the shortest and longest TFs. Results from PX were not significant.

EXPERIMENT 2

Blakemore, Nachmias and Sutton (4) found that significant aftereffects can be produced by inspection gratings up to 35° orientation from the vertical. Experiment 2 was concerned with the effects of adaptation on the perceived orientation of TFs. The hypothesis under consideration was that prolonged exposure to an IF of a particular orientation will cause a perceptual change in the perceived orientation of a TF to the degree that these two figures stimulate the same orientation selective mechanism.

Classical explanations predict a monotonic decrease in the amount of displacement as the amount of tilt is increased. This prediction follows from the assumption that contour displacement mechanisms, such as those involved in lateral inhibition, are sensitive to the distance between objects. Further, the amount of displacement should be the same for all TFs since the contour distance remains constant.

However, the multiple mechanism explanation predicts that each of the IFs will activate a specific distribution of activity in the population of orientation detecting mechanisms. Since these mechanisms are also sensitive to the
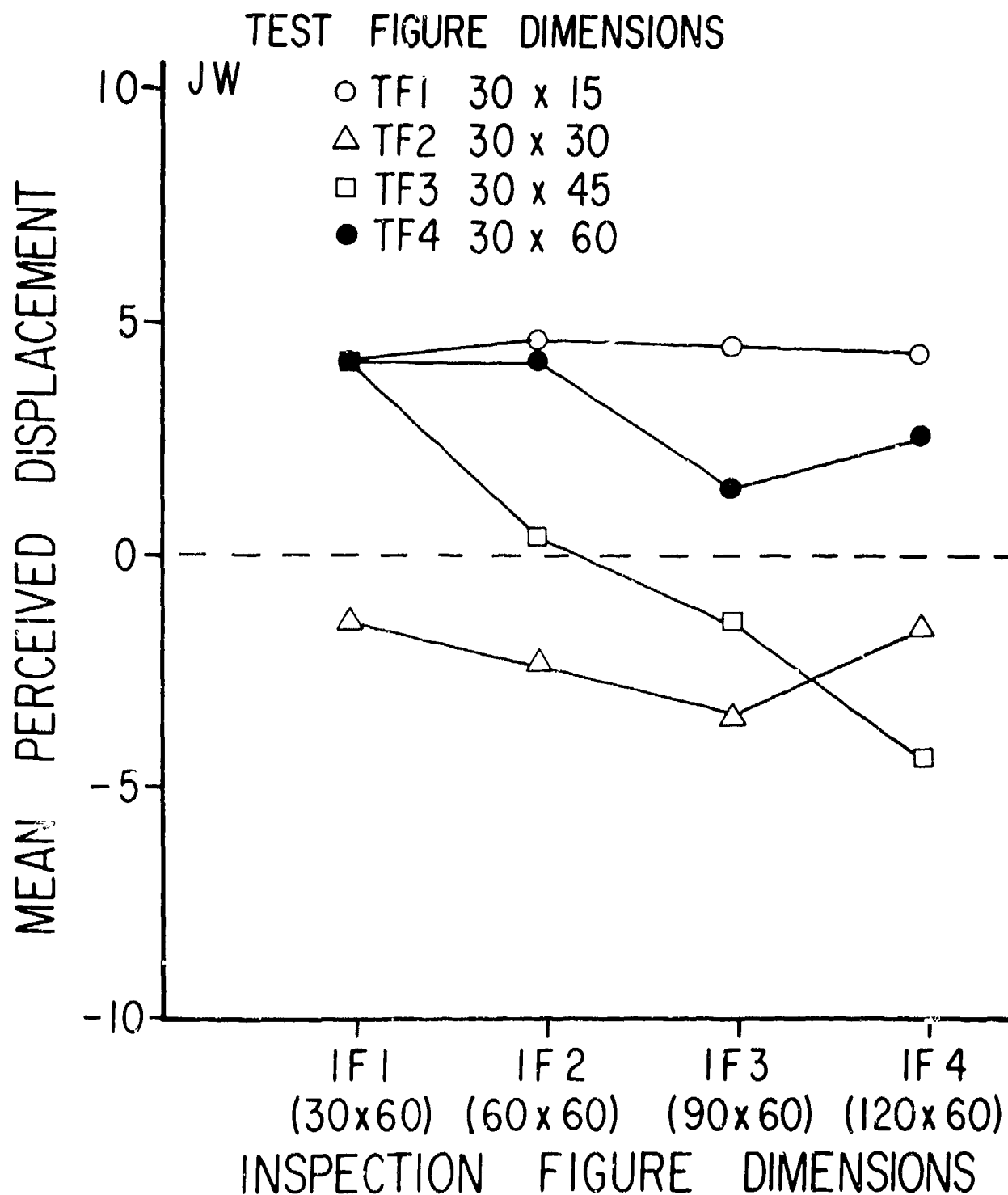
Figure 3. Mean perceived displacement (average difference scores as a function if inspection figure (IF) dimensions for different test figure (TF) dimensions for S̲ JW.

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Figure 4. Mean perceived displacement (average difference scores as a function of inspection figure (IF) dimensions for different test figure (TF) dimensions for S KW.
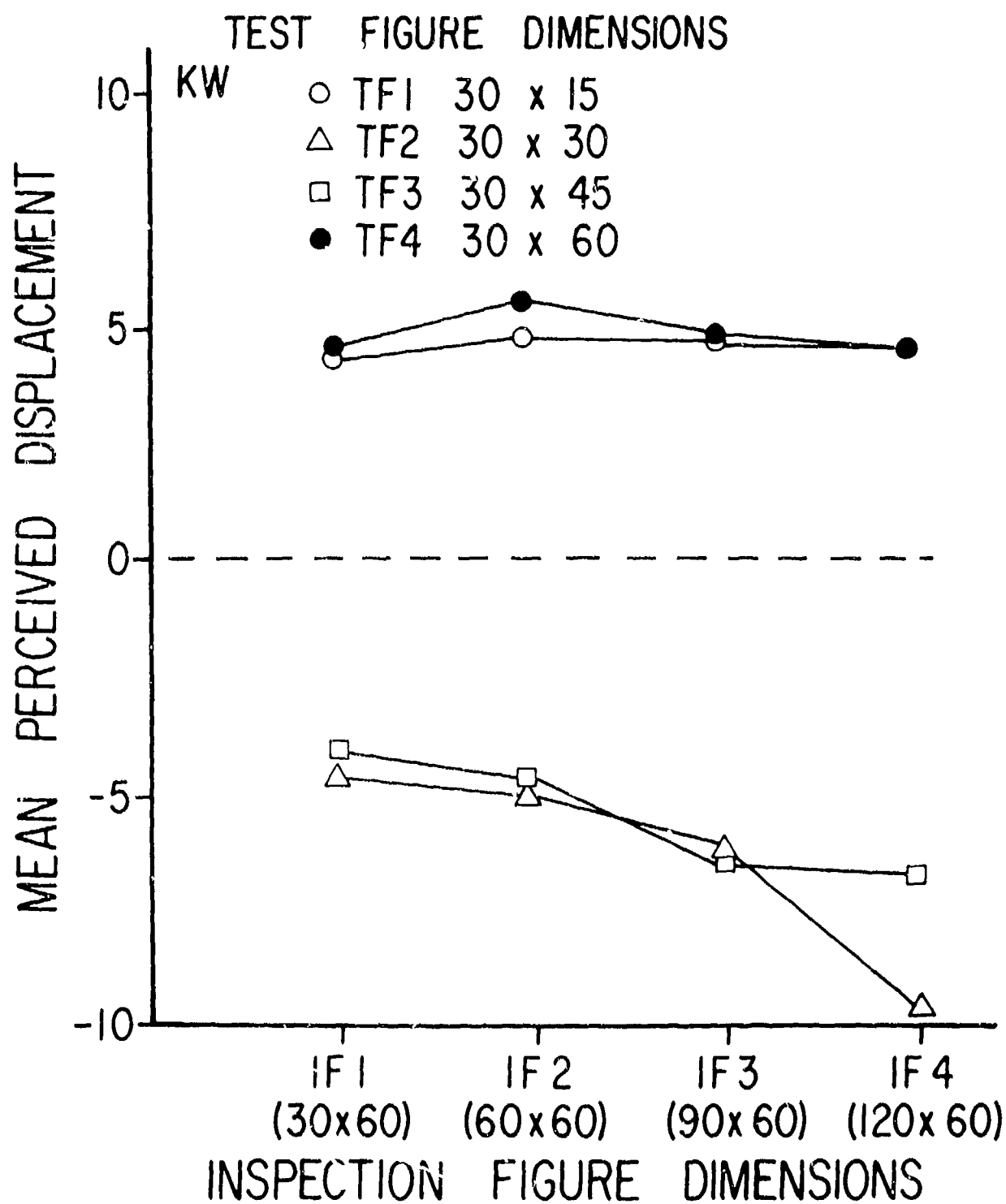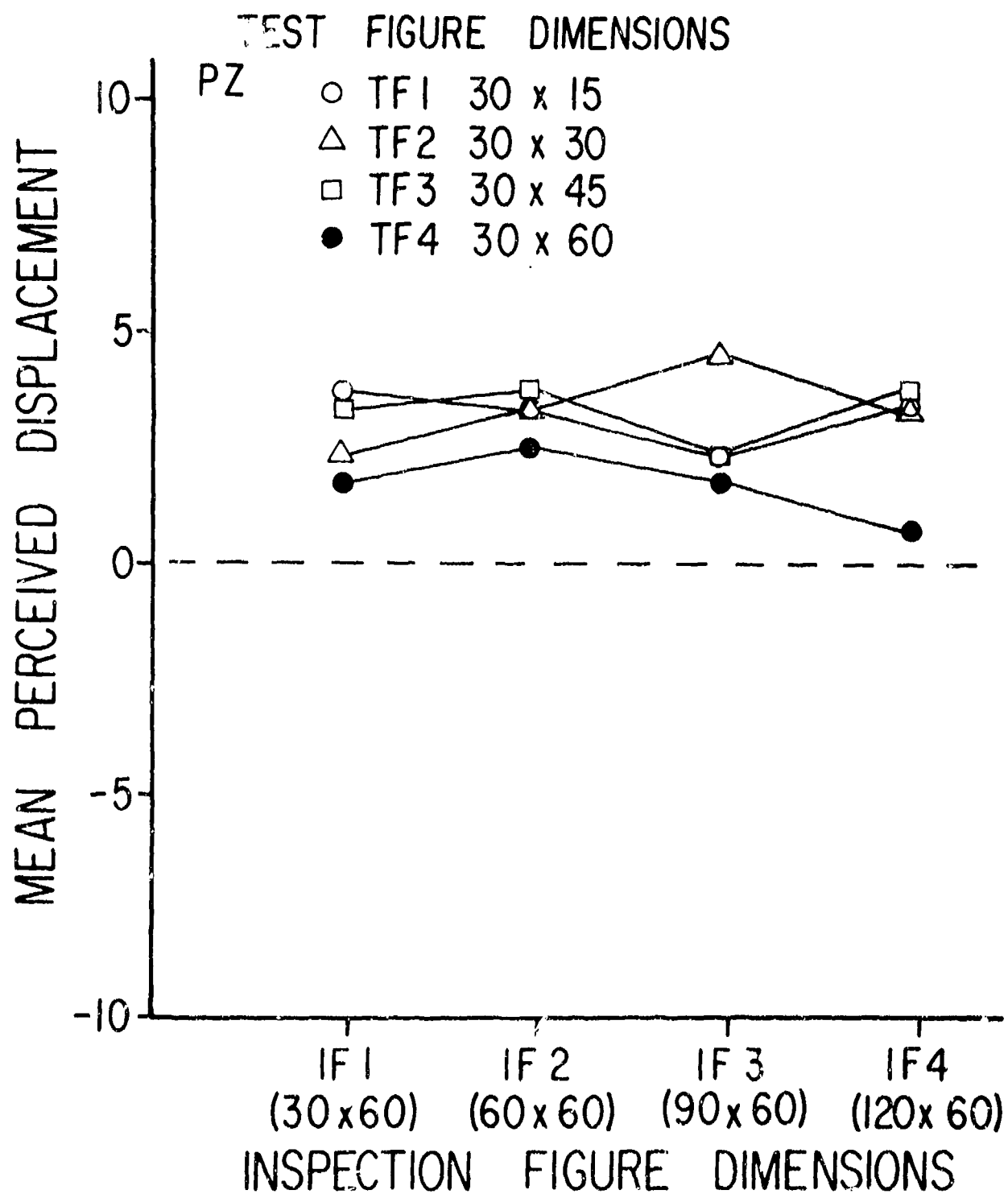
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Figure 5. Mean perceived displacement (average difference scores) as a function of inspection figure (IF) dimensions for different test figure (TF) dimensions for S PZ.

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dimensions of stimulus objects, the magnitude of the aftereffect will be specific not only to the particular IF, but also to the size of the TF. In a vertical orientation no aftereffect should be noted since adaptation does not affect the neuron's characteristic orientation. Classical explanations make this same prediction based on the principle that figures which fall within the contours of the IF are not displaced.

METHOD

Stimuli.

The IFs and TFs were homogeneous patches of light subtending a maximum of 1^0 of visual angle. The size of the IFs was held constant at 60 min high by 20 min wide and were positioned at 90^0, 105^0, 120^0, and 135^0 in the subject's visual field. In the text, these conditions will be referred to in terms of their deviation from vertical; that is, 0^0 (IF1), 15^0 (IF2), 30^0 (IF3), and 45^0 (IF4). The TFs differed in width from 15 (TF1) to 30 (TF4) Min. of arc in 5 min. increments and were oriented at 0^0, or vertical. A range of 900 to 1800 min^2 of visual angle was subtended on the retina.

Procedure.

Experiment 2, two subjects (BW, JS) were used. Using a process of selective adaptation Ss were presented with an IF of a particular orientation and then with a series of four TFs. In all IF conditions the TFs were placed such that the contour distance between the two figures remained constant. In the 0^0 condition the vertical separation remained constant while in the remaining three conditions the angular separation between the two figures remained constant within each condition. In Experiment 2 the concern was with the effects of adaptation on the perceived orientation of the TF, which in all cases was objectively 0^0 (vertical).

The psychophysical method used in the experiment was an orientation rating procedure. Following adaptation to an IF of a particular orientation Ss were required to rate the perceived orientation of each TF. Each S was first presented with a series of control conditions which differed from the subsequent experimental sessions in that there was no prior adaptation to an IF before an estimation of orientation was made. Further details of the experimental procedure are identical to Experiment 1.

Results.

Data were transformed by determining the geometric mean of orientation judgments and are reported as the amount of perceived displacement from vertical.

Prior to each experimental session Ss made a series of unadapted judgments of the orientation of the TF. In all cases they judged the orientation to be 90, or 0^0 from vertical.

Figure 6 contains the mean perceived displacement obtained in the adapting conditions. Each curve shows the apparent orientation for the TFs in the various IF conditions. The higher the point on the curve, the greater is the FAE for that TF size. Note that the amount of aftereffect is different, i.e., a different apparent orientation, depending upon the orientation of the IF. The largest aftereffects were
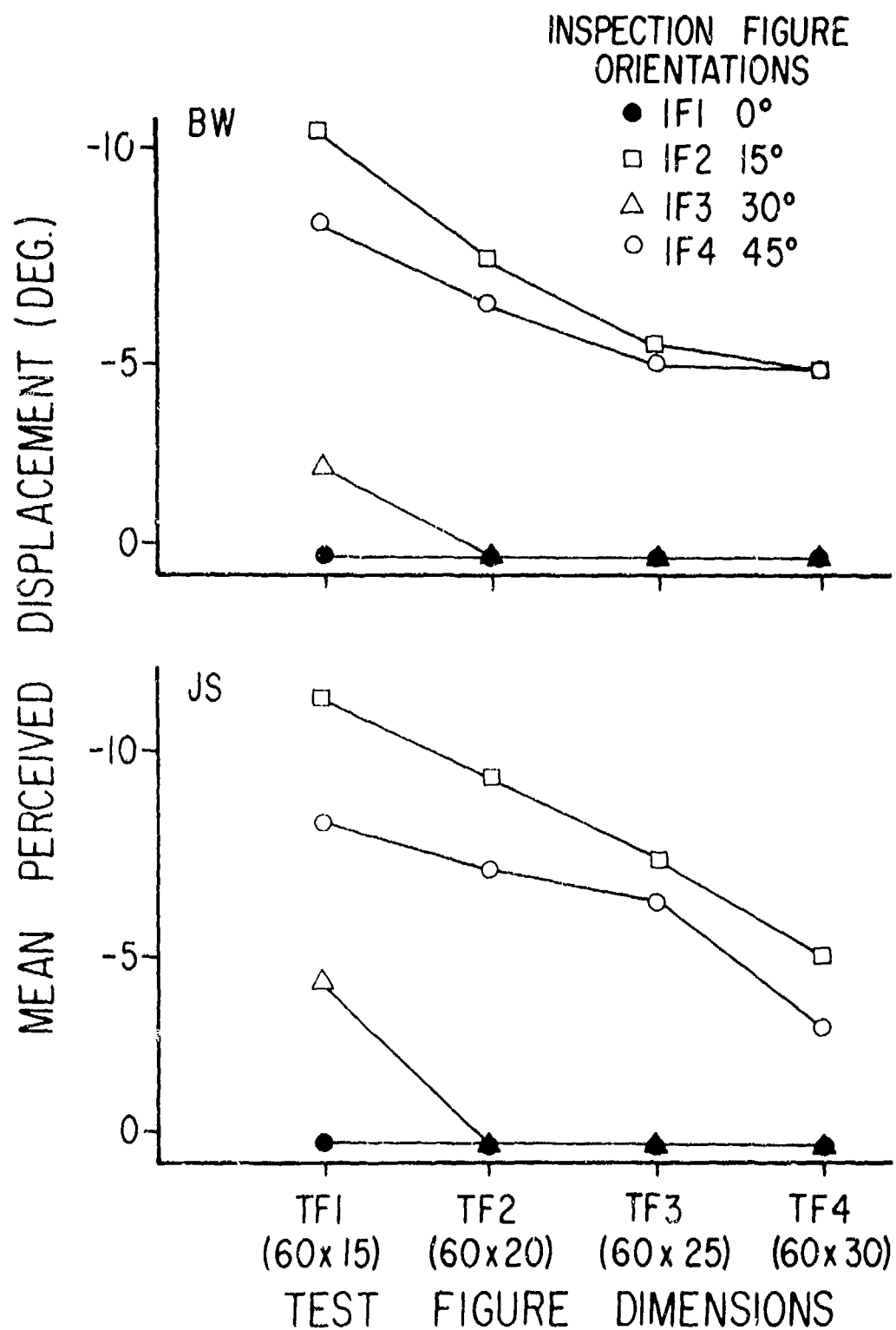
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Figure 6. Mean perceived displacement (average difference scores) as a function of test figure (TF) dimensions for different inspection figure (IF) orientations.

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noted in the 15° and 30° conditions. No aftereffects were noted in the 0° condition where the orientation of the IF was objectively the same as that of the TF. Also, little or no effect was noted in the 45° conditions.

Repeated measures ANOVAs were calculated to determine the significance of the aftereffect. The results contained interactions, both for BW, $F (9, 9) = 6.897$, $p < .01$, and JS, $F (9, 9) = 11,980$, $p < .001$). Analyses of the simple main effects for BW (IF2, $F (3, 9) = 40.740$, $p < .001$; IF3, $F (3, 9) = 12.366$, $p < .01$) and JS (IF2, $F (3, 9) = 45.396$, $p < .001$; IF3, $F (3, 9) = 24.956$, $p < .001$; IF4, $F (3, 9) = 8.190$, $p < .01$) suggest that the amount of aftereffect noted in a particular IF condition is also due in part to the width of the TF.

In a 3x4 repeated measures ANOVA, there were significant interactions between IF and TF for BW, $F, (6, 9) = 4.328$, $p < .05$, and JS, $F (6, 9) = 8.256$, $p < .01$. The 0° condition was eliminated from this analysis on theoretical grounds, since both multiple mechanism and classical explanations predict the same outcome for that condition.

Discussion

The results from these experiments can be regarded as evidence that the visual system contains neurons which are sensitive to the size and orientation of retinal images. Also supported is Blakemore and Sutton's (3) idea that the classical figural aftereffects can best be explained in terms of the relative activities of mechanisms tuned to specific stimulus parameters. Perceived displacement was not solely a function of the contour distance between the two objects as postulated by the classical explanations of the FAE phenomenon. This conclusion is drawn from the finding that a constant FAE was not noted at some fixed contour distance when the contour separation was either a vertical or orientation displacement.

One possible explanation for these results, consistent with Blakemore and Sutton's (3) multiple mechanism hypothesis, is that the IFs in both these experiments changed the distribution of activity in the population of size and orientation detecting mechanisms. For the most part the displacements noted following adaptation were like those obtained by Blakemore and Sutton.

In Experiment 1, no significant changes were produced in the appearance of the largest and smallest TF. The perception of the largest TF was not changed since the adaptation process does not affect the size to which the neuron is most sensitive. The smallest TF was also relatively unchanged following adaptation - a finding consistent with the fact that selective adaptation does not affect the perception of objects outside the range of the IF. These findings suggest that the visual system treats both repetitive and non-repetitive patterns in the same manner.

Further evidence against the existing explanations of FAE is obtained by examining the pattern of displacement for each TF over the IF conditions. Classical explanations predict that the magnitude of the FAE will increase monotonically as the area of the IF increases since the amount of flux is also increasing. Therefore, a flux effect is confounded with the displacement effect. However, the flux effect was not found in the present experiment. In fact, in a few instances the amount of aftereffect decreased following adaptation to the largest TF.

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Similar differences in the perception of TFs following adaptation to IFs of different orientation were obtained in Experiment 2. Different apparent orientations for each TF were obtained for each IF orientation. One interpretation of these results is that the mechanisms under consideration are at the cortical level of the visual system. This interpretation is consistent with Maffei, Feorentini and Bisti (17) who found that the major site of adaptation is at the cortical level, as well as with electrophysiological studies of ganglion and LGN cell receptive fields which have been shown to be concentrically arranged. Another possible explanation is that adaptation is occurring at subcortical regions which in turn affects the function of cortical cells. Or, the adaptation may be occurring at both levels. However, regardless of which interpretation is correct, these results provide evidence against Ganz' hypothesis (9) that the FAE is solely a result of lateral inhibitory interactions at the level of the retina and are consistent with those results obtained by Blakemore and Sutton.

Classical explanations would predict that the magnitude of displacement would be the same within each IF condition since the contour distance between the two figures remains constant. Also, the amount of displacement noted within each TF condition should be constant as the IF ranges from 0^0 to 45^0. The results of the present experiment, however, indicate that the amount of aftereffect noted was also dependent upon TF width, since the amount of the aftereffect declined as the TF grew wider. In general, the greatest amount of perceptual distortion occurred for those TFs narrower than the IFs. One possible explanation for these findings is that the narrower TFs fall completely within the range of these size and orientation selective mechanisms. Even in the 45^0 condition, a slight aftereffect was noted for the narrowest TF. The presence of an interaction between IF and TF demonstrates that the empirically obtained functions for the different IF conditions are not parallel. If the classical explanations were correct the change in aftereffect should be the same within each IF condition.

Results suggest that the mechanisms under consideration are sensitive to orientation over a range of 30^0, since the largest aftereffects were noted in the 15^0 and 30^0 conditions. These findings are consistent with those obtained by Blakemore et al. (4), but not with other psychophysical studies dealing with orientation selectivity. Campbell and Kulikowski (5), e.g., noted that the range of these mechanisms is from 12^0 to 15^0. The results from the present experiments also suggest that the mechanisms which mediate orientation judgments are the same as, or are operating in conjunction with, those mechanisms which mediate size judgments.

It might be argued that despite precautions against the occurrence of afterimages, they nonetheless occurred. However, the presence of afterimages does not account for the size and orientation selectivity observed in the experiments. Since the exposure of the IF preceded all the trials the same aftereffect or afterimage was present during all test intervals. Thus, the only difference in the type of stimulation was that stimulation produced by the TF. Whether the phenomenon noted in the present experiment was an aftereffect or an afterimage, the fact remains that each TF was differentially changed following adaptation. Therefore, it may be concluded that the changes in the appearance of the TF resulted from the degree to which those mechanisms mediating the detection of IFs affected those mechanisms which mediate the detection of TFs.

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The present study is important in that it suggests an alternative explanation of FAE. Results indicate that when using a paradigm based on multiple mechanism explanation, selective changes both in the size and orientation of objects are observed following adaptation. In addition, the results suggest that in the processing of other suprathreshold phenomena the visual system acts as a multiple channel, a finding consistent with psychological and electrophysiological threshold studies.

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As an alternative to the classical explanation of figural aftereffects (FAE), it was hypothesized that FAE are due to changes in the relative activities of multiple mechanisms tuned to specific features of the stimulus pattern. Changes along the stimulus dimensions of size and orientation were studied. The rationale was that prolonged exposure to an inspection figure (IF) of a particular size or orientation would change the appearance of a test figure (TF) to the extent that these two

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figures stimulate the same mechanism. Following selective adaptation to a particular IF, subjects were required to make size or orientation judgments with the size or orientation of the IF serving as the anchor for these judgments. Results indicated that there was a particular range of TF size or orientation over which a given IF would produce perceptual changes. TFs outside this range were not affected. Findings were compared with the classical explanation and the role of multiple mechanisms as a basis of FAE was elaborated